

Recent Developments in Hominoid Ontogeny: An Overview and Summation

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In 1993, we organized and co-chaired a symposium on hominoid ontogeny at the 62nd annual meeting of the American Association of Physical Anthropologists in Toronto, Canada. This volume grew out of that symposium. Our initial aim was to assemble individuals working in a number of areas of hominoid ontogeny in order to see how new analyses and data could contribute to our understanding of the evolutionary and functional biology of hominoids. We also hoped that the symposium would facilitate comparisons within and between hominoid taxa. The contributions contained here have done all these things. They also raise provocative new questions and hypotheses regarding 1) the role of ontogeny in reconstructing hominoid evolution, 2) the range of intraspecific variation in extant hominoid ontogeny, 3) the documentation of unequivocal interspecific differences in ontogeny among extant hominoids, 4) potential relationships between the growth and development of differing developmental systems, and 5) the role of heterochrony in hominoid evolution.

Anthropologists have long understood the importance for our understanding of human evolution of documenting ontogeny (see Wood, this volume) in our hominoid relatives and ancestors. Perhaps the greatest contribution of ontogenetic data for human evolution occurs when it is placed in a comparative perspective to address taxonomic and phylogenetic questions. Aspects of demography (e.g., determining age at death of fossils) and socioecology (e.g., the development of sexual dimorphism among extant hominoids) are

best understood in the light of comparative ontogenetic data.

The development of the teeth initially appeared to hold the greatest promise of enhancing our understanding of hominid ontogeny and evolution. Using extant hominoids for comparison, tooth emergence, calcification patterns, and incremental histological patterns of teeth have been utilized to estimate age, rate, and timing of maturation in extinct hominids (see Macho and Wood, in press; Beynon and Dean, 1987, 1988; Bromage, 1987; Dean, 1987a,b; Dean et al., 1993; Mann, 1975; Mann et al., 1990; Ramirez-Rozzi, 1993; Smith, 1992; Wolpoff et al., 1988). Despite the successes achieved by these studies, persistent doubts continue to be voiced concerning the validity of the methodologies used to study teeth, the comparability of different data sets, and the small sample sizes found in most studies of great ape dental development (as well as in some studies of humans: see Tompkins, this volume) and their failure to investigate the range of intrapopulation and interpopulation differences. The use of dental developmental patterns to infer growth rates and degree of maturation is itself dependent on our still imperfect understanding of how pattern, rate, and maturation co-vary (see Macho and Wood, in press; Smith, 1992; and contributions in this volume).

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Although the patterns of tooth development correlate well with at least some of the other developmental events of primate life history (Smith, 1992), other maturation events are less easily predicted from patterns of dental development. In addition, the changes which have occurred during the evolution of hominoid tooth developmental patterns and rates are more complex than originally thought. The differences in these patterns between various hominoid taxa do not appear to be explained by simple heterochronic changes (neoteny, acceleration, or retardation), nor are they independent of developmental changes in other somatic systems (Macho and Wood, *in press*; Wood, *this volume*).

This volume includes new information relevant to the debates mentioned above on rate and pattern of odontogenesis but also contains information on the ontogeny of other somatic systems in an attempt to provide a more integrative picture of hominoid ontogeny. Wood opens this volume by recognizing the stimulus of Adolph Schultz's lifelong efforts to document primate morphology, variation, and development (Schultz, 1924, 1930, 1936, 1940, 1941, 1956, 1963). Wood raises several important questions regarding the theoretical contributions of primate comparative development to understanding human evolution, and briefly reviews some of the ways in which studies of primate ontogeny have increased that understanding. In discussing the relevance of the concept of heterochrony, Wood notes that simple heterochronic change is inadequate to explain the variety of modifications that have occurred in hominoid evolution. Citing the example of cranial base morphology, he argues that "the cranial base of adult modern humans is . . . not explicable as a generalized paedomorphic phenomenon. . ." and concludes that it is perhaps only for the teeth and face that we have begun to understand the mechanisms of growth and development. Noting that even in this area "there is considerable scope for . . . further study," Wood raises several questions to challenge future researchers, reiterating the need for broader comparative data ("an appropriately comprehensive and detailed comparative framework") to interpret the hominid fossil record and hominoid evolution.

Godfrey and Sutherland's paper raises provocative questions about the relationships between size, shape, and the rate and timing of development in the context of human evolution. The authors clarify the sometimes bewildering morass of heterochronic terminology that was developed since Gould's (1977) influential work on ontogeny, and provide a comprehensive and challenging review of Gould's heterochronic clock model and of other recent work by other authors (e.g., Shea, McKinney, and McNamara). Godfrey and Sutherland translate Gould's clock graphs into multivariate matrices divided into size (growth parameter), shape (developmental parameter), and age (maturation parameter). They then use these matrices to derive predictions about changes in growth allometries, developmental events, and the resulting morphological changes between ancestors and descendants.

Godfrey and Sutherland also review how allometry has been used and misused in evolutionary studies, including the relationship between heterochrony and allometry. They re-examine how developmental retardation changes slopes and intercepts of growth allometries. They then discuss whether neoteny is congruent with the evidence of human evolution, using vectors and matrices to model the changes necessary for the conditions of neoteny. They assert that neoteny "will stand or fall as an explanation for human paedomorphosis to the extent that it can be shown that, in human ontogeny, somatic retardation exceeds germinal retardation." They conclude that critics of Gould (1977), who have argued that human growth patterns "do not match the requirements of Gould's own clock graph depicting neoteny," have erred "in their derivation of the expectations of Gould's clock model."

Godfrey and Sutherland also explore the relationship between allometry, timing, and human evolution. They assert that some of the previous analyses of allometric heterochrony were flawed in assuming uniform changes in relative growth rate and in dismissing a relationship between the timing and rate of development. "The argument that neoteny does not predict a mosaic of changes in rates of relative growth reflects a poor understanding of how slow develop-

ment translates into changes in the slopes of growth allometries." They conclude that in order for a descendant to equal the size of a mature ancestor while retaining juvenile shape, the growth rates of individual traits must be affected differently. They concur with Gould (1977) that changes in developmental rate will affect the timing of somatic developmental events.

Leigh and Shea continue to investigate the nature of ontogenetic processes in their paper on the ontogeny of variation in body size within and among African apes. In addition, they explore the life-history consequences of the different growth strategies employed by male and female gorillas, chimpanzees, and bonobos. A series of elegant regression analyses demonstrates that the ontogenetic processes leading to adult size in African apes vary. They suggest that gorillas are larger than chimpanzees and bonobos because gorillas grow at consistently faster rates. Differences in both rate and duration of growth account for size differences between the two species of *Pan*, with rate differences being especially pronounced between females. Sexual dimorphism in body size results from differences either in the duration of growth (*Gorilla* and *Pan paniscus*) or in the rate of growth (*Pan troglodytes*).

Having established the variable nature of the development of body size among African apes, Leigh and Shea go on to evaluate the hypothesis of Janson and van Schaik (1993) that a slow growth rate is a risk-averse strategy in social primates. They find general agreement between the predictions of this model and the socioecological research and growth data on African apes. Behavioral data indicate high ecological risk among female common chimpanzees and very low ecological risks among both male and female gorillas. Janson and van Schaik's predicted negative correlations between ecological risk and growth rate is supported by the high growth rates in gorillas and the very low rates among female common chimpanzees.

In their paper, Simpson, Russell, and Lovejoy explore the developmental and ontogenetic factors that produce relative differences in lengths and limb proportion between chimpanzees and humans. They calculate average total long-bone lengths for cross-sectional samples of multi-age (infant

to adult) Native Americans and wild-shot chimpanzees. Their results indicate that when the data are normalized for growth period differences, chimpanzees and humans present similar patterns of growth of the humerus and ulna. The relative onset and cessation of elongation, the duration, and the relative rate of growth for these two upper limb bones in both species is the same: "Chimpanzees and humans adhere to different absolute schedules yet maintain the same relative developmental schedule." They conclude that for the ulna "humans, with their shorter ulnae, attain this length by elongating it at a slower relative rate than the humerus."

Their results also indicate that absolute growth rates of the femur and tibia are similar for chimpanzees and humans, but when normalized for growth and duration differences, human femora and tibiae elongate at faster relative rates than those of chimpanzees. They conclude that their results demonstrate "multiple pathways" to the different limb proportions between the two species and that differences in the growth rate between the two species begin early in ontogeny.

The two papers by Tompkins in this volume present new evidence of variability in tooth calcification between human populations, and between living and fossil hominid populations. In the paper on human population variability in relative dental development, Tompkins compares mandibular tooth calcification in a cross-sectional sample of black South Africans, Native Americans, and French Canadians of European descent. He tests for statistical differences between the samples, repeatedly comparing differences using all teeth and most calcification stages of each tooth as successive relative reference points. He also documents sex differences in calcification in the French Canadian and in the African sample. The results indicate that the Africans and Native Americans display varying patterns of advancement of relative dental development of M2 compared to the French Canadians. The most striking difference, however, was in the M3 comparisons. The African sample was significantly advanced in M3 calcification compared to the French Canadians and also (to a lesser degree) to the Native Americans. There are also some indications that the

French Canadian females are advanced in canine development compared to the females in the other population samples.

Tompkins situates these patterns of variation within the broader context of genetics, developmental rates, and morphological correlates of tooth calcification rates. Reviewing earlier studies that have documented differences in relative calcification patterns between teeth, Tompkins concludes that "the results of the present study demonstrate that population differences in dental eruption and calcification schedules are due in part to differing patterns of relative development between teeth." He proposes that the most likely explanation for the differences seen in molar calcification is that the French Canadians have molar calcification rates like those of the Africans but longer periods between initiation of the calcification of successive molars. He goes on to suggest that the differences in relative dental development may be related to interpopulation differences in jaw size. He also suggests that there may be a potential relationship between relative molar development and the rapidity of skeletal maturation, discussing this in light of the evidence for skeletal advancement in populations of African descent.

The data that Tompkins presents in this paper "provides a solid basis for comparing fossil hominid patterns of relative dental development to the range of variability in modern humans." He proceeds to make these comparisons in his second paper in this volume by comparing Upper Pleistocene dental development with the modern human sample of the previous paper. His Upper Pleistocene sample includes 29 Neandertal/archaic *Homo* and 61 Upper Paleolithic specimens. His results indicate that the fossil hominids are advanced in M2 compared to the French Canadians of European descent but not to the black South Africans. The fossil hominids are also advanced in M3 development compared to the French Canadians but, whereas there is some evidence of advancement in the Neandertal sample compared to the South Africans, the Upper Paleolithic sample is not significantly different from the African population. The results also indicate that the fossil hominids are delayed in rela-

tive I1 and P3 development compared to recent humans. He comments that this delay in I1 and P3 seen in the fossils is similar to the pattern seen in comparisons of apes and modern humans, suggesting that delayed relative incisor and first premolar calcification is the plesiomorphic condition for hominoids.

In both of these papers, Tompkins proposes that variability in relative molar development could be due to differences in tooth/jaw relationships or may reflect differences in potential skeletal maturation between human populations. Since the fossil groups are most similar to the South Africans, he suggests that these fossils possess similar genetic potential for skeletal maturation (see discussion above). He further suggests that the similarity seen between the fossil hominids and the modern African population supports the hypothesis that no significant differences existed between the hominid samples in the length of their growth periods and between either hominid group and modern humans.

The papers by Anemone, Mooney, and Siegel; Kuykendall and Conroy; and Kuykendall provide valuable new comparative material on chimpanzee dental development with relevance for the evaluation of dental development in fossil hominids. With the publication of these papers, the numbers of chimpanzees of known age which have been studied radiographically total 168 (Anemone et al., 1991 [N = 16], plus the papers in this volume). With the wealth of new data provided by these papers for both tooth emergence and calcification in captive chimpanzees of known age, there is no longer a need for workers to rely on Dean and Wood's (1981) venerable dental developmental chart for chimpanzees (based on wild-shot museum specimens of unknown age). Close overall agreement between the work of Kuykendall's and Anemone's groups (in spite of differences in samples, methods of data collection, and of data analysis) suggest that their results are robust and that clear differences in both pattern and timing of chimpanzee and human dental development are now clearly demonstrated.

The paper by Anemone et al. presents clear evidence that chimpanzees differ from

humans in the temporal overlap in calcification of the adjacent molar crowns and in advanced molar development relative to the anterior teeth. Humans are characterized by the presence of a temporal gap of several months to several years between the complete calcification of a molar crown and the beginning of calcification of the next (i.e., distal) molar in the jaw. A different pattern is seen in chimpanzees in which a distal molar crown begins to calcify before the molar mesial to it has completed crown calcification. Compared to humans, chimpanzees also show advanced molar development relative to anterior tooth development. That is, at a comparable point in anterior tooth development (i.e., emergence of the central incisor), chimpanzee molars are developmentally advanced over human molars. The evolutionary significance of these pattern differences is that they allow us to distinguish between "apelike" and "human" patterns of dental development from radiographs or CT scans of the jaws of immature fossil hominids. Anemone and his coauthors make a strong case for apelike dental development and, by inference, apelike life history patterns (Smith, 1988) among Plio-Pleistocene hominids based on Conroy and Vannier's (1991a,b) CT scans of South African australopithecines.

Contrary to previous reports (e.g., Dean and Wood, 1981; Simpson et al., 1990), Kuykendall documents sex differences in canine development over several consecutive calcification stages (females are advanced over males). He comments "these patterns of sex differences suggest that there may be biologically meaningful differences in canine developmental timing between male and female chimpanzees." In addition, Kuykendall establishes ratios for proportional crown and root formation times in chimpanzees, comparing them to the same data for humans. His results indicate that only the molars demonstrate "greater periods of both crown and root formation in humans compared to chimpanzees."

As discussed above, Kuykendall's paper on the timing of dental calcification presents results which are in close agreement with those of Anemone et al. (1991, this volume). For instance, Kuykendall's results support the contention of Anemone et al. that there are clear

differences between chimpanzees and humans after initial stages of calcification in development of the anterior teeth relative to M1. His results also indicate that "although the absolute durations of tooth formation are in some cases quite similar, the dissimilarity in chimpanzee and human crown-root ratios indicates that relative differences in development exist for some teeth."

Although there is close similarity with Anemone et al. (1991, this volume), Kuykendall's results in his paper on the timing of tooth calcification stages do differ in indicating 1) a slightly later time period for root completion in the incisors, 2) a slightly earlier time period for canine crown initiation, 3) an earlier time period for premolar crown completion, and 4) a later time period for molar root completion. Kuykendall suggests that these differences may be due either to differences in methodology and sampling or to normal variability in tooth development between different populations (see discussion of paper by Marzke et al., below). Kuykendall also cautions that although differences do appear to exist between human and chimpanzee patterns of molar development, "the differences are not as great as those observed for other teeth . . . , and they alone do not clearly distinguish between human and chimpanzee dental development patterns." Kuykendall's results are valuable in indicating a relatively wide range of developmental stages for a tooth type in any year age class, leading him to conclude that the range of normal variability makes precise age estimates difficult.

The paper by Kuykendall and Conroy documents variation in the patterns and polymorphisms of tooth calcification in the chimpanzee, using the same sample as in Kuykendall's paper on calcification timing. Although their results are very similar to previous descriptions of tooth calcification in the chimpanzee (Anemone et al., 1991; Dean and Wood, 1981; Conroy and Mahoney, 1991), they do find polymorphisms in the patterns, although the only one to reach significant levels was between the canine and the premolar/M2 group. They caution that some dental emergence sequence polymorphisms do not necessarily occur at significant levels in tooth calcification (and vice

versa), concluding that "tooth calcification and tooth emergence polymorphisms are to some degree independent." However, their results do reiterate earlier indications that the I1/M1 sequence polymorphism does not exist in either emergence or calcification sequences in the chimpanzee. This remains a difference from humans. Kuykendall and Conroy further note that the developmental relationships among teeth change throughout tooth calcification, which may "confound attempts to make interspecific distinctions at some, but not all, stages of tooth calcification." They note that this has implications for attempts to sort out ape versus modern human patterns.

The paper by Marzke et al. on chimpanzee dental emergence and growth in this volume has important implications in documenting differences between colonies with different environmental parameters. They note that their study documents "variability in chimpanzee growth and development rates that has not been shown in previous studies." Their results reinforce the need to be aware of potential environmental effects on whatever ontogenetic parameter is being studied. The paper is based on a mixed longitudinal study of growth and development (weight, hand/wrist maturation, and dental emergence) of 175 chimpanzees from three different captive environments. The data has been analyzed with LOWESS curve-fitting techniques. Results indicate 1) a clear trend for differences between colonies for weight with some of the differences being significant, 2) significant differences between mother-reared and hand-reared animals for weight, 3) more rapid maturation (hand/wrist) (although not significantly different) in some colonies than others and with hand-rearing rather than mother-rearing, 4) some evidence of sex differences in maturation (for some comparisons, the difference is significant), and 5) some evidence of sex differences in tooth emergence. The authors suggest that these data provide a more detailed set of growth norms for comparison and elucidation of developmental status of fossil hominoids. "Evidence in this study . . . has implications for the application of data from living captive chimpanzees to estimation of tooth emergence status in fossil speci-

mens. . . . Tooth emergence curves for mother-reared captive chimpanzees may be more applicable to this purpose than curves generated from data on hand-reared captive animals."

The paper by Winkler on the appearance of ossification centers in a cross-sectional sample of immature orangutans and chimpanzees presents new data on skeletal development and its variation in these hominoids as well as information on a neonatal gorilla. Winkler explores a possible relationship between skeletal development and dental development, but as previously reported for primates (Lewis and Garn, 1960; Nissen and Riesen, 1949a,b), there is no evidence of a strong relationship in this sample. Study results suggest a stronger relationship between skeletal development and weight. The study is particularly useful in greatly expanding published information on epiphyseal appearance in the orangutan (sample ages range from birth to age 4) and the range of variation present in the developing systems. For instance, this study is the first to establish a partial sequence of carpal ossification in the orangutan. She compares carpal ossification sequences in the orangutan, chimpanzee, and humans, commenting that tarsal ossification sequences appear more similar between these extant hominoids than that of carpals. She also notes that "the neonates here . . . demonstrate greater variability than indicated by previous studies."

The final paper in the volume by Winkler et al. is a continuation of a previous paper published in 1991 by the same authors and presents data on development of the permanent dentition in the orangutan. The authors are particularly interested in presenting data on variation in the patterns of tooth development and alveolar emergence in this ape, after emergence of the M1. Their cross-sectional sample includes 89 specimens in which they examine dental development in both the upper and lower jaws. Statistical comparisons of tooth pair stages in isomeres of the upper and lower jaws of individuals in their sample indicate isochrony, lending support to earlier work (Dean and Wood, 1981) that found few qualitative differences in the development of upper and lower tooth pairs in the great apes. In many ways, re-

sults presented in this paper closely corroborate earlier results of Dean and Wood (1981) on great ape dental patterns, but results here do indicate greater variability in the orangutan patterns than previously reported. This variation includes 1) variation between teeth in patterns of crown stage development, 2) variation in root development (relative root length and size varies substantially between orangutans of the same emergence status), 3) variation in the degree of sequential molar crown overlap, and 4) variation in emergence patterns. The authors also note differences in the developmental timing and patterns of teeth in the orangutan compared to published reports for the chimpanzee (Anemone et al., 1991; Dean and Wood, 1981).

As the papers in this volume amply demonstrate, we have made enormous strides in the construction of a comparative database on the ontogeny of hominoids. However, our ability to understand ontogeny and life history among fossil hominids is limited by the quality of the available data on developmental timing and pattern among living primates, especially on subjects of known chronological age. Much work remains to be done, and we would like to close this essay (and this volume) with some of our thoughts on the current state of the art and trends and goals of research on hominoid ontogeny.

We believe that Godfrey and Sutherland's contribution to this volume will stimulate a vigorous discussion about the role of neoteny in human evolution. The publication of this thought-provoking paper will surely stimulate further work on heterochronic processes and their importance in studies of primate sexual dimorphism, allometry, and socioecology.

Perhaps the key area in which studies of ontogeny have contributed to our understanding of human evolutionary history involves dental development and the reconstruction of life history traits of fossil hominids. This volume includes papers which provide standard radiographic techniques, and methods of data collection and analyses which will facilitate further studies of hominoid dental development in the future. However, additional research is needed in several areas. While common chimpan-

zees have been relatively well studied, much work remains to be done on the other great apes. Similarly, we know a great deal about dental development in middle-class Caucasian children in North America, but our information on other human populations is limited. The determination of interindividual variation in pattern and timing of dental development in apes and humans is another area which also still requires a great deal more research. We need to fill all of these gaps in our database before we can ever claim to truly understand the nature of dental development among hominoids, and to use this understanding to its fullest potential in answering questions of evolutionary significance.

One area of research in the ontogeny of fossil hominid teeth bears special notice for its great promise and potential: the analysis of incremental markings in the microstructure of dental enamel and dentine. These incremental markings, reflecting circadian and circaseptan secretion patterns (Dean, 1987a,b; Macho and Wood, in press), allow investigators to measure absolute periods of development and to deduce age at death of fossil material. Some of the most interesting work in this area has been done by two researchers who presented papers as part of the Toronto symposium but are not represented as part of this volume, Tim Bromage (Hunter College, CUNY) and Fernando Ramirez-Rozzi (CNRS, Paris). In an earlier study, Bromage (1991) demonstrated the temporal periodicity of enamel microstructural markers through the use of *in vivo* fluorescent staining of dental tissues in *Macaca nemestrina*. Ramirez-Rozzi's (1993) ongoing studies of incremental markers in naturally fractured teeth of the Omo hominids may elucidate both developmental and taxonomic questions regarding these fossils.

Finally, this volume demonstrates that work on skeletal development and that of other physiological systems is only now beginning to be fully integrated with the evidence from dental development. An integrative and holistic view of development in a wide range of systems (e.g., dentition, skeleton, sexual), which are linked together by an understanding of the genetic and endocrinological factors that coordinate and control

these processes, is obviously a long term goal for researchers of hominoid ontogeny. During the last year of her life, Elizabeth S. Watts was working on just such a synthesis of growth and development among primates. We will unfortunately never see the work that Elizabeth had hoped would be the culmination of her distinguished research career in primate growth and development. It will eventually fall to someone else to attempt the intellectually challenging task of synthesizing our understanding of primate ontogeny. We hope that in some small way this volume has helped speed the day when this task can be successfully completed.

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